THE EPIDERMAL STRUCTURE OF THE CARBONIFEROUS GYMNOSPERM FROND *RETICULOPTERIS*

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ABSTRACT. The epidermal structure of Upper Carboniferous *Reticulopteris* fronds is documented for the first time. It is shown to be very similar to that of *Neuropteris obliqua*, confirming earlier stratigraphical and gross-morphological evidence of a phylogenetic link between the two frond-types. The evolution of *Reticulopteris* fronds with their anastomosed venation from typical open-veined *Neuropteris* probably reflects the drier climate in the middle Westphalian. *Barthelopteris* gen. nov. is proposed for the Stephanian and Autunian species ‘*Reticulopteris*’ *germarii*, which has a very different epidermal structure from type *Reticulopteris*.

THE trigonocarpaleans form a group of gymnosperms abundantly represented in the Upper Carboniferous fossil record. They were mainly shrubs and smaller trees that favoured drier habitats such as raised levée-banks, within equatorial swamps. One of the few exceptions is a liana-like trigonocarpalean recently reconstructed from coal ball petrifactions (Hamer and Rothwell 1988). The foliage, which is the part of the plant most commonly found fossilized, consisted of large dissected leaves superficially resembling fern fronds. These leaves were mostly between 0·5 and 2 m long, although examples up to 7 m long have been reported (Laveine 1986). In most form-genera, the ultimate segments of the fronds (usually referred to as pinnules, thus continuing the analogy with fern fronds) had a venation consisting of a midvein from which were emitted simple or dichotomous lateral veins. In a few cases, the venation was anastomosed.

One such frond-type with reticulate veining belongs to the form-genus *Reticulopteris* Gothan, 1941. This was established for reticulate-veined fronds, which in all other characteristics resemble the imparipinnate neuropterids. It is of particular interest as being the only example of a reticulate-veined frond that can be directly linked with a non-reticulate ancestor, through a reasonably convincing phylogenetic model: the transition from *Neuropteris obliqua* (Brongniart) Zeiller, through *N. parvifolia* Stockmans and *N. semireticulata* Josten, to *Reticulopteris muensteri* (Eichwald) Gothan documented in the Westphalian record by Josten (1962) and Laveine (1967).

The position of *Reticulopteris* as a reticulate-veined counterpart of *Neuropteris* was until recently relatively straightforward and unchallenged. However, the taxonomy of neuropterids has been revised by Cleal *et al.* (1990) using new evidence of frond architecture and epidermal structure. Where there was originally just one form-genus, at least five can now be clearly identified and delineated. The question thus arises, of which of these form-genera (if any) is *Reticulopteris* the reticulate-veined counterpart? The Josten (1962) model clearly suggests a link with *Neuropteris* in its restricted sense, as *N. obliqua* has recently been shown to belong there (Cleal and Shute 1992). Establishing phylogenetic relationships using stratigraphical distributions can be risky and should normally be supported by more concrete morphological evidence. Frond architecture is in this case of little help, since no large specimens of *Reticulopteris* with critical features have been reported, and so epidermal structure appears the only way of resolving the problem.

Cuticles from the type species of *Reticulopteris* are documented to see if they confirm the taxonomic position suggested by the Josten model (Josten 1962). They were prepared from specimens from Cape Breton Island, Nova Scotia, Canada, which has previously proved a good area for Carboniferous cuticle studies (Cleal and Zodrow 1989). Bell (1938) first recognized and

mapped the stratigraphical range of *R. muensteri* from the Maritime Provinces of Canada, describing specimens from the Sydney Coalfield, with later records coming from the Pictou Coalfield (Bell 1940) and New Brunswick (Bell 1962). Most recently, specimens have been reported from the small Mabou Mines Coalfield (Zodrow and Vasey 1986) and it is these that form the basis of the present study.

MATERIAL AND METHODS

Specimens studied are from the Mabou Mines Coalfield on the west coast of Cape Breton (Text-fig. 1). The stratigraphy is summarized in Text-figure 2, and further details are in Zodrow and Vasey (1986). The entire section is fossiliferous, *R. muensteri* being particularly abundant in the roof rocks of the coals and in the silty shale lithologies. The specimens described in this paper are all from the lower Westphalian D.

The specimens are preserved in an extremely soft matrix. Many are naturally macerated, with little more than the cuticle remaining, resulting in a very low colour-contrast between fossil and matrix. Obtaining good photographs of hand specimens thus proved extremely difficult. To document details of venation, we prepared transfers using the method of Walton (1923).
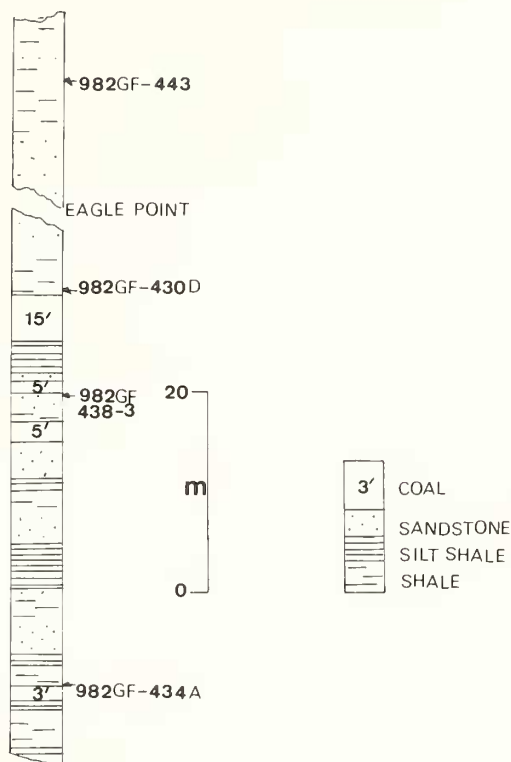
Cuticles were prepared from a specimen (University College of Cape Breton Collections, Number 982GF-443) which still retained some carbonized phytoleim. Naturally macerated cuticles in the Upper Carboniferous rarely preserve details of the epidermal structure. The matrix was removed by hydrofluoric acid. The fossils were then macerated in Schulze's Solution for about three hours and then washed in 5 per cent ammonium hydroxide and finally in distilled water. The cuticles were mounted in glycerine jelly containing safranin on
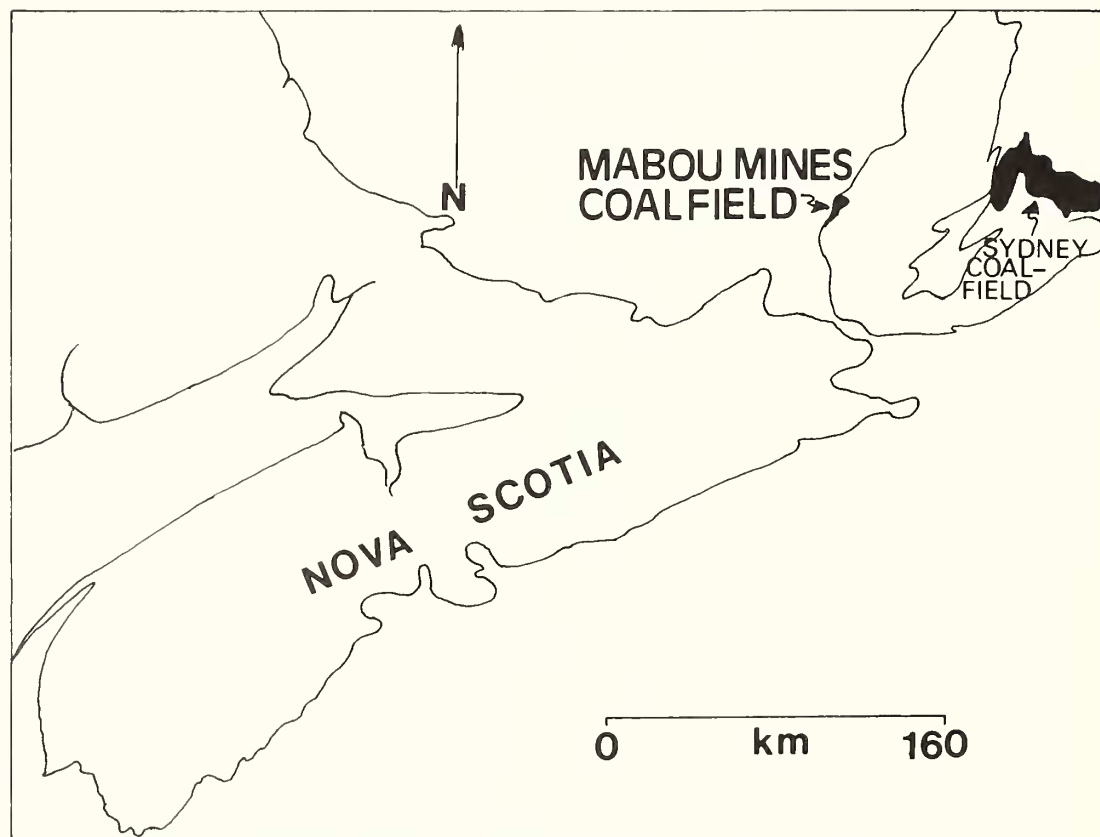
TEXT-FIG. 1. Outline map of Nova Scotia, showing location of Mabou Mines Coalfield.

glass slides. The slides were examined under a Leitz Ortholux II microscope, using both brightfield and Nomarski (interference phase) illumination. Fourteen slides were prepared, and are stored in the collections of the University College of Cape Breton.

TEXT-FIG. 2. Lithostratigraphical section through Mabou Mines Coalfield, showing horizons where the described specimens were found. Based on Zodrow and Vasey (1986, fig. 1).

982GF–443

EAGLE POINT

982GF–430 D

15′

5′ 982GF 438–3
5′

20

m

0

982GF–434 A
3′

3′ COAL
SANDSTONE
SILT SHALE
SHALE

DESCRIPTIONS

Gross morphology

The material consists mainly of isolated pinnules, or of small fragments of ultimate pinnae. Rachides are thick and longitudinally striated. Pinnae are more or less parallel-sided and terminated by a single apical pinnule. Apical pinnules are all about 10 mm long and may either be elongate and subtriangular (5 mm wide) or more isodiametric and rhomboidal (10 mm wide).

Lateral pinnules are quite variable in shape, but can be grouped into two broad categories. The most common are oval to linguiform, up to 25 mm long and 10 mm wide (Text-fig. 3A). Near the pinna apex they are broadly attached to the rachis; lower in the pinna they have a more constricted base, being attached to the rachis by only a narrow band of lamina on either side of the midvein, and often with an acroscopic auricle. These are probably the pinnules from the main part of the frond, above the main dichotomy.

Pinnules of the second category are larger, up to 60 mm in length, with a rounded to subtriangular aspect. These are probably the forma *impar*-type pinnules from the basal parts of the frond.

The venation pattern is shown in Text-figure 4. The midvein enters the pinnule on the basiscopic side. It initially lies at a low angle to the rachis, until it reaches the centre of the pinnule. It then bends and extends along the long axis of the pinnule. In the smaller pinnules near the pinna apex, the midvein extends for about 50% of the pinnule length; in the larger pinnules lower in the pinna, it extends for about 90% of the length.

The lateral veins are attached to the midvein at 10–20°, and are loosely anastomosed (Text-figs 3B–C,4). The anastomoses are produced in three different ways:

1. by undulating or highly flexuous veins approaching each other but remaining separate by several cell-widths (i.e. pseudoanastomoses);
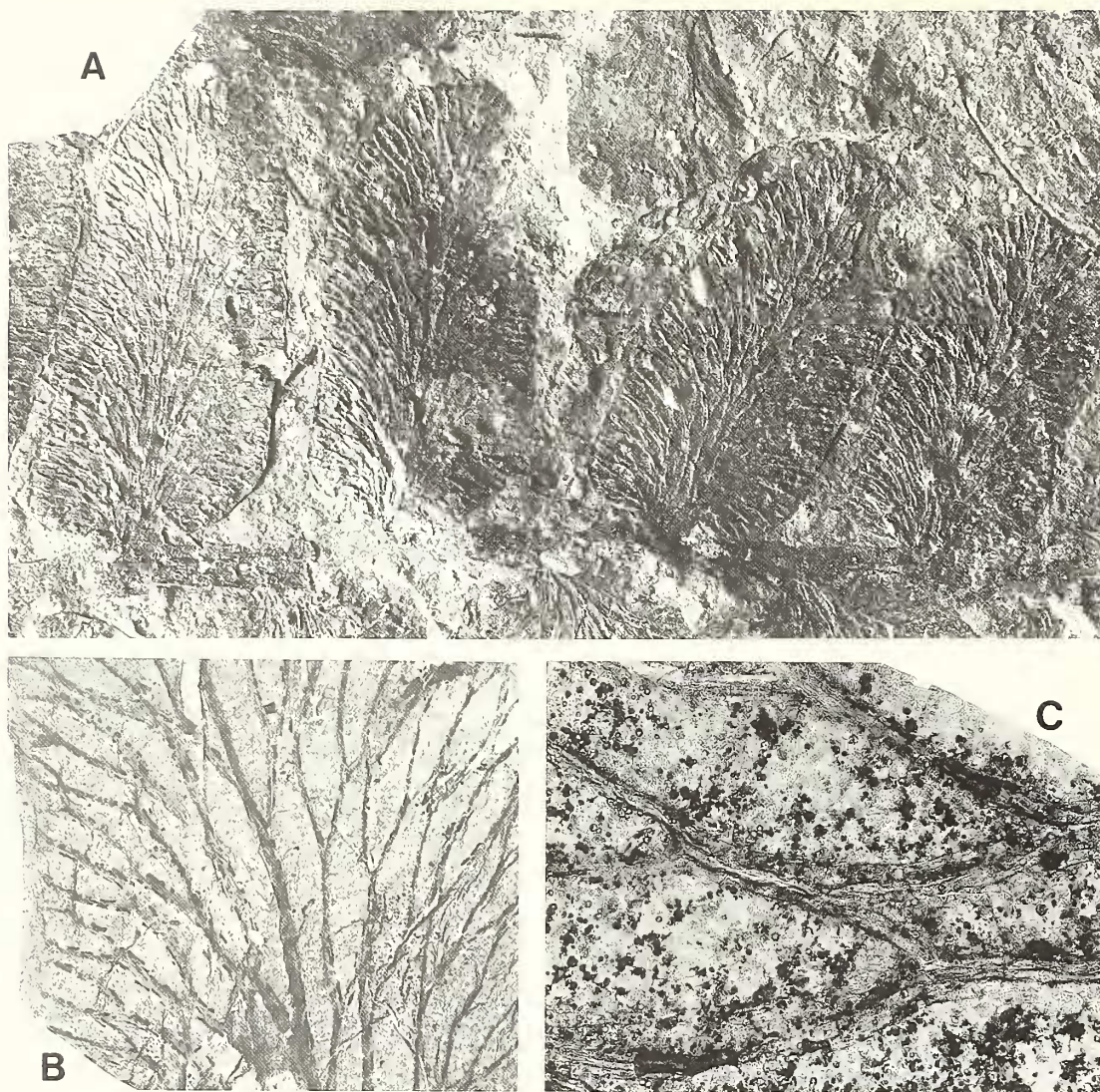
TEXT-FIG. 3. *Reticulopteris muensteri* (Eichwald) Gothan. Features of gross morphology. A, UCCB, 982GF-438-3; unmacerated specimen, showing shape and venation of pinnules, × 6. B, UCCB, 982GF-434A; naturally macerated pinnule, separated from rock, showing detail of venation, × 25. C, UCCB, CCB/982GF-443/4; pinnule macerated in Schulze's solution but not washed with alkali, showing close-up of venation, × 50.

2. by tangential anastomoses, where the veins come into intimate contact;
3. by full anastomoses, where the veins appear to cross over on contact.

Anastomosis types 2 and 3 predominate in the larger pinnules; in the smaller pinnules, type 1 are more common, especially on the acroscopic side of the pinnule. The veins meet the pinnule margin at about right-angles, and produce a vein density of 4·5–5·0 per mm. Further details of the variation in the venation in these specimens are in Zodrow and Vasey (1986).
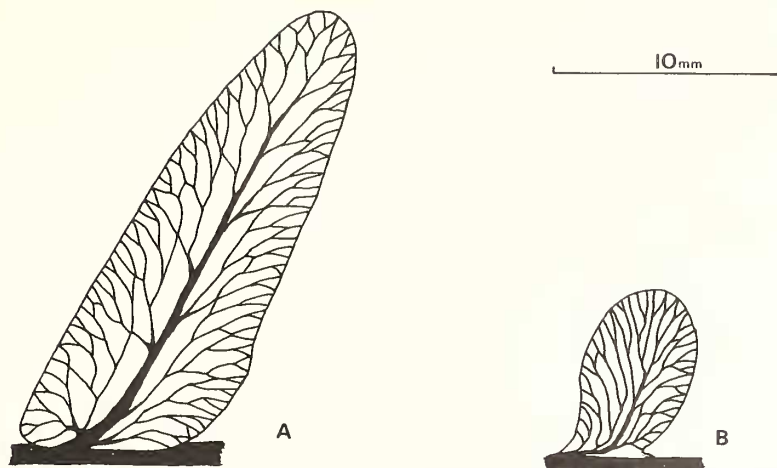
TEXT-FIG. 4. *Reticulopteris muensteri* (Eichwald) Gothan. Venation diagrams, based on Zodrow and Vasey (1986, fig. 8). A, fully developed pinnule. B, small pinnule from near pinna apex.

Cuticles

The adaxial epidermis is differentiated between the costal and intercostal fields (Pl. 1, fig. 1; Text-fig. 5A). Costal cells are elongate and subrhomboidal, up to 200 μm long and 20 μm wide. Intercostal cells are significantly shorter and more irregularly polygonal, up to 120 μm long and 30 μm wide (Pl. 2, fig. 1). No trichomes were observed. Two examples of small, round structures, 20 and 25 μm in diameter, were observed attached to intercostal cells on one cuticle. The larger of the two is damaged and shows little structure. The other seems to be ovoid with a central fold (Pl. 2, fig. 6). The nature of these structures is unclear.

The abaxial epidermis is also differentiated between the costal and intercostal fields (Pl. 1, fig. 4; Text-fig 5B). Costal cells are elongately subrhomboidal, up to 160 μm long and 30 μm wide. Intercostal cells are irregularly polygonal and more or less isodiametric, up to 35 μm in size (Pl. 2, fig. 2). Most of the intercostal cells are neighbour cells to the stomata (Pl. 2, fig. 2). The cuticle covering the costal cells seems often to be in a different plane to the intercostal cells (Pl. 1, fig. 3). However, it is unclear whether the stomatiferous areas were sunken, or there is merely a taphonomic wrinkling of the cuticle, perhaps reflecting differential cuticle thicknesses in different parts of the pinnule.

Trichome bases 25–30 μm in diameter are present on the abaxial cuticle (Pl. 2, fig. 5). They are sparsely distributed and occur mainly but not exclusively in the costal fields. There also seems to be a greater concentration of hair bases near the pinnule margin. No trichomes were found attached, but they evidently had a splayed base and were often attached to the middle of a single epidermal cell.

Stomata are anomocytic and restricted to the intercostal fields of the abaxial epidermis (Pl. 2, figs 2–4). In some parts of the abaxial cuticle, the cuticle of the guard cells is lost and all that remains is a hole (Pl. 1, fig. 2). Where preserved, however, they show the guard cells to have been about 25 μm long and 6 μm wide (Pl. 2, fig. 4). The alignment of the polar axes of the guard cells is somewhat irregular, but there seems a general tendency for them to be arranged parallel to what is probably the long axis of the pinnule (Text-fig. 5B). Some stomata seem to be covered by a small fold of cuticle, which may be the remains of a stomatal pit (Pl. 2, fig. 3).

COMPARISONS

Neuropteroid taxa

In the revised classification of neuropteroid foliage form–genera proposed by Cleal *et al.* (1990), the cuticles clearly indicate that *R. muensteri* lies closest to *Neuropteris sensu stricto* (i.e. the Group II species of Cleal and Zodrow 1989). Particularly significant characters are: (1) clear differentiation between costal and intercostal fields on the adaxial cuticle; (2) well-developed anticlinal walls on the
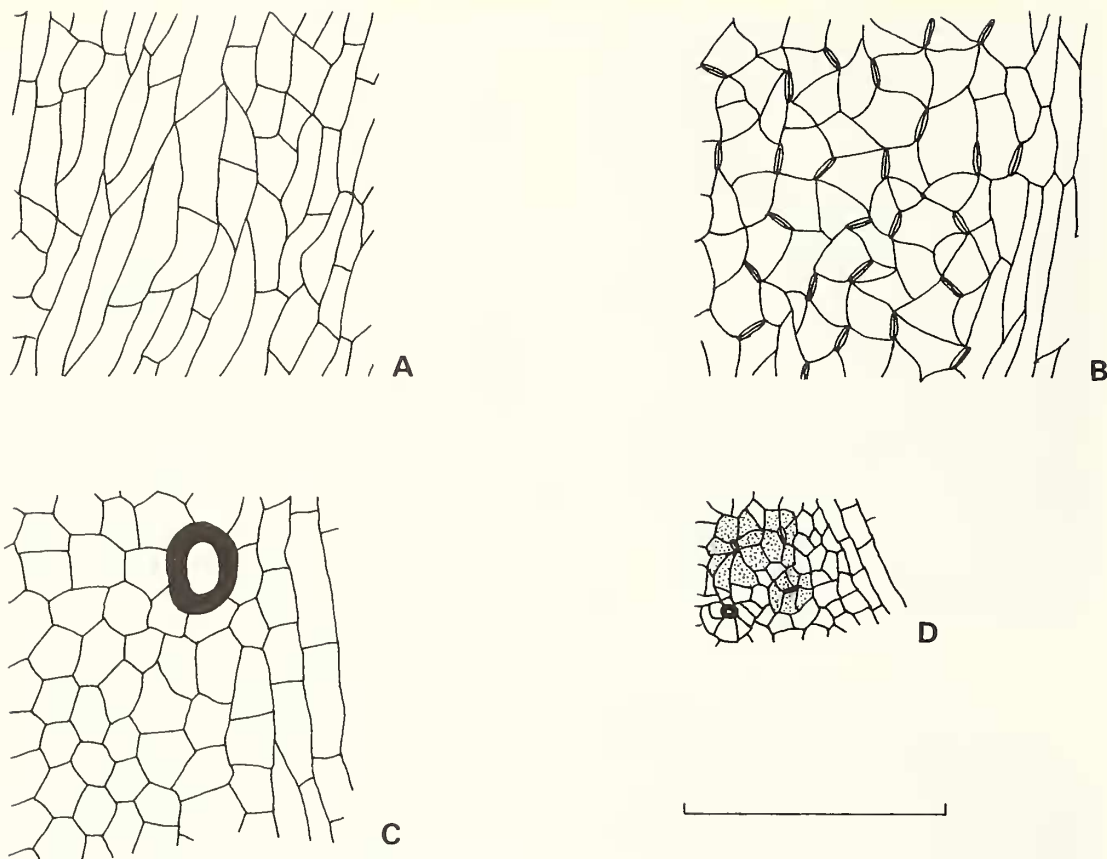
TEXT-FIG. 5. Epidermal features separating *Reticulopteris* from *Barthelopteris*. A–B, *Reticulopteris muensteri* (Eichwald) Gothan. UCCB, CCB/982GF-443/1, drawn directly from slides using camera-lucida; Westphalian D, Mabou Mines Coalfield, Nova Scotia. A, adaxial cuticle. B, abaxial cuticle, showing stomata without subsidiary cells. C–D, *Barthelopteris germarii* (Giebel) Zodrow and Cleal, comb. nov. Based on Barthel (1962, figs 45–46). C, adaxial cuticle showing hair base (in black). D, abaxial cuticle showing stomata with subsidiary cells (stippled) and hair base (in black). Scale bar = 200 μm.

abaxial cuticle; (3) anomocytic stomata; and (4) presence of multicellular trichomes on the abaxial cuticle. In contrast, the laveineopterids show an essentially uniform distribution of epidermal cells on the adaxial surface, and have no trichomes with poorly-cutinized anticlinal walls on the abaxial surface. Both the macroneuropterids and neurocallipterids are readily distinguishable from

EXPLANATION OF PLATE I

Figs 1–6. *Reticulopteris muensteri* (Eichwald) Gothan. Cuticles photographed using brightfield illumination; Westphalian D; Mabou Mines Coalfield, Nova Scotia. 1, UCCB, CCB/982GF-443/1; adaxial cuticle, × 100. 2, UCCB, CCB/982GF-443/3; abaxial cuticle showing relationship between costal and intercostal field, × 100. 3, UCCB, CCB/982GF-443/7; abaxial cuticle including midvein area in upper part of figure, × 100. 4, UCCB, CCB/982GF-443/1; abaxial cuticle showing stomata with missing guard-cells, × 100. 5, UCCB, CCB/982GF-443/7; adaxial cuticle, × 100. 6, UCCB, CCB/982GF-443/3; abaxial cuticle showing stomata with guard-cells, × 100.

PLATE 1

ZODROW and CLEAL, *Reticulopteris*
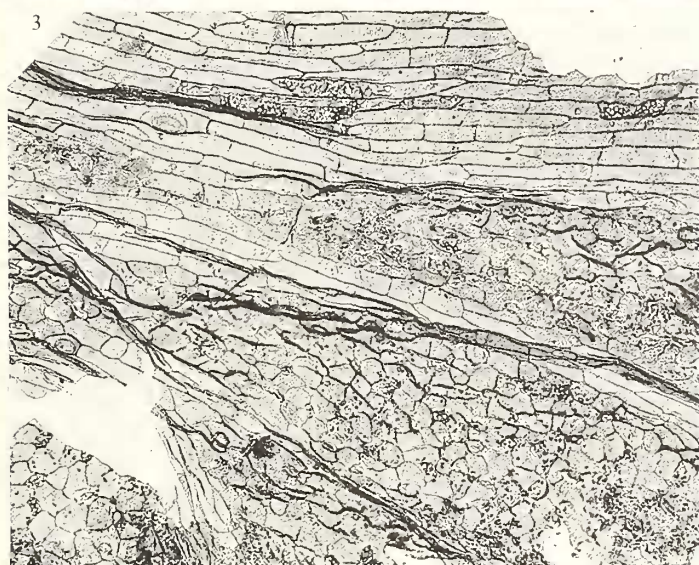
R. muensteri by their stomatal apparatuses having from two to four well-developed subsidiary cells in the brachyparacytic, or rarely, cyclocytic arrangement.

Other reticulopterids

Only one other well-documented species has been assigned to *Reticulopteris* – namely *R. germarii* (Giebel) Gothan. It is known from the upper Baruellian to the Autunian of Portugal, Spain, France, Italy, Germany and Yugoslavia (see Wagner 1964, for further details of its distribution). Cuticles have been described by Barthel (1962, 1976).

    R. germarii has some of the obvious, gross morphological characters of *Reticulopteris*, including lateral pinnules with a constricted base, an anastomosed venation, and pinnae terminated by a single apical pinnule (Gothan 1941; Barthel 1958, 1976). The venation is far more consistently anastomosed over the entire width of the pinnule, with none of the pseudo- or tangential anastomoses that occur so commonly in *R. muensteri*, but this could be due merely to the venation of the later species having reached a more 'advanced' condition. However, the differences in epidermal structure are far more marked (Text-fig. 5). According to Barthel (1962), the adaxial epidermis of *R. germarii* is virtually undifferentiated between the costal and intercostal fields, except for the midvein, while on the abaxial epidermis the stomata are cyclocytic. Prominent trichome bases were reported on both sides of the pinnule, particularly near the midvein, but no attached trichomes were found.
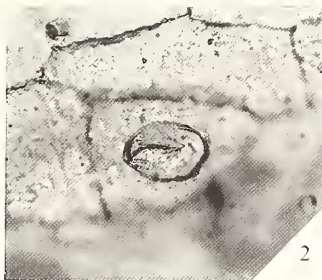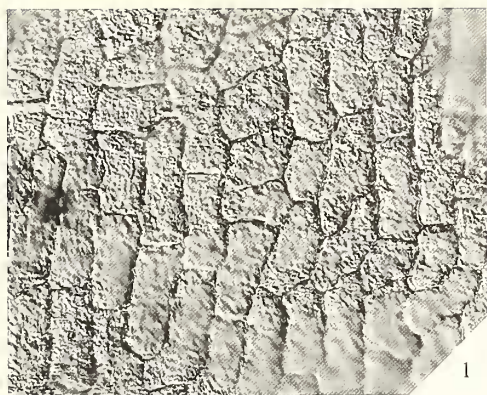
    The epidermal structure of *R. germarii* in fact stands far nearer to that of *Neurocallipteris* Sterzel *emend.* Cleal *et al.*, 1990, than that of *R. muensteri*. According to Cleal *et al.* (1990), the neurocallipterids have an adaxial epidermis with weakly differentiated costal and intercostal fields, and stomata on the abaxial epidermis that are cyclocytic or amphicyclocytic. There are differences, most notably the presence of prominent papillae on the abaxial epidermis of neurocallipterids. However, there are clearly more similarities than differences in the epidermal structures of the two taxa. There is furthermore an interesting correlation in the general shape and symmetry of the *R. germarii* pinnules with one of the species currently assigned to *Neurocallipteris*, i.e. *N. planchardii* (Zeiller) Cleal *et al.*, 1990. For instance, a large fragment of a *R. germarii* frond figured as a drawing by Langiaux (1984, fig. 228) compares closely with photographs of *N. planchardii* in Reichel and Barthel (1964, pl. 1, fig. 1; pl. 4, figs 1–2) and Vetter (1968, pl. 34, figs 1, 7–8). Such relatively subtle characters of pinnule form would not normally be considered of taxonomic significance at the rank of form-genus but, taken together with the cuticular evidence, the similarities cannot be ignored. Thus, gross morphological, cuticular and stratigraphical evidence all point to *R. germarii* being a mesh-veined analogue of *Neurocallipteris*, rather than being a true reticulopterid (i.e. a mesh-veined analogue of *Neuropteris*). For this reason, a formal proposal is made below to transfer *R. germarii* to a new form-genus, *Barthelopteris*.

SYSTEMATIC PALAEONTOLOGY

The classification of supra-generic taxa follows that of Cleal (in press), and incorporates the satellite-taxon

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PLATE 2

ZODROW and CLEAL, *Reticulopteris*

concept outlined by Thomas and Brack-Hanes (1984). The synonymy lists, which are not complete, use the system of annotations summarized by Matthews (1973) with two additions. One is specific to palaeobotany, and is the prefix of the letter 'k' to a synonym if it includes cuticular evidence. The second is of more general use; entries prefixed by the dagger sign (†) are the most recent references which include a reasonably full synonymy and extensive illustration.

Class CYCADOPSIDA Barnard and Long, 1975
Order TRIGONOCARPALES Seward, 1917 *emend*. Meyen, 1984
Satellite form-genus RETICULOPTERIS Gothan, 1941 emend.

p*1941　　*Reticulopteris* Gothan, p. 427.
　†1967　　*Reticulopteris* Gothan; Laveine, p. 215.

Type species. Reticulopteris muensteri (Eichwald) Gothan, 1941, p. 428.

Emended diagnosis. Pinnules entire-margined, oval to linguiform, with lateral margins parallel or slightly tapered. Pinnule apex round or slightly acuminate. Pinnule base cordiform, generally narrowly attached to rachis, but sometimes more broadly attached, particularly high in a pinna. Midvein usually extends for half to two-thirds the pinnule length, except in the largest pinnules, where it extends for most of the pinnule length. Lateral veins clearly marked, anastomosed, with dimension of the meshes diminishing towards the pinnule margin. Ultimate pinnae terminated by single apical pinnule. Frond probably bipartite, each primary segment being tri- or occasionally quadri-pinnate with intercalated monopinnate segments attached to the two primary rachis branches. Adaxial foliar epidermis clearly differentiated between costal and intercostal fields. Well-developed anticlinal walls on abaxial foliar cuticle. Anomocytic stomata found only in intercostal fields of abaxial epidermis. Multicellular trichomes on the abaxial epidermis.

Remarks. The above emended diagnosis is adapted from that given by Laveine (1967), with the addition of the foliar epidermal details. The nomenclature of frond architecture follows that of Cleal and Shute (1991).

Reticulopteris muensteri (Eichwald) Gothan, 1941, emend.

Plates 1–2; Text-figs 3–5A–B

　*1840　　*Odontopteris Münsteri* Eichwald, p. 87, pl. 3, fig. 2.
　1849　　*Dictyopteris Münsteri* (Eichwald) Brongniart, p. 19.
　1862　　*Dictyopteris Hoffmanni* Roemer, p. 29, pl. 7, fig. 3.
　1868　　*Dictyopteris cordata* von Roehl, p. 50, pl. 15, fig. 6; pl. 21, fig. 7*b*.
　1880　　*Dictyopteris rubella* Lesquereux, p. 145, pl. 23, figs 7–10.
　1899　　*Linopteris Münsteri* (Eichwald) Zeiller, p. 48, pl. 4, fig. 13.
　1913　　*Linopteris major* Goode, p. 265, pl. 27, figs 1, 3.
　1941　　*Reticulopteris Münsteri* (Eichwald) Gothan, p. 428.
　†1967　　*Reticulopteris münsteri* (Eichwald) Gothan; Laveine, p. 218, pls 58–60; pl. 61, figs 1–4.

Type specimen. Holotype figured with protologue originated from a sandstone exposed in the Lougan Mine, Donets Coalfield, Ukraine. Stratigraphical details were not given, but the specimen probably originated from the lower Moscovian. Its present location is unknown.

Emended diagnosis. Pinnules oval to elongately linguiform, sometimes somewhat triangular, 6–25 mm long, 4–8 mm wide; obliquely attached to rachis. Midvein flexuous and extends for up to two-thirds the pinnule length, except in the larger pinnules near the base of the frond where they extend for most of the pinnule length. Near the midvein, lateral veins are pseudoanastomosed or form only large meshes; nearer the pinnule margin, veins are more fully anastomosed, producing smaller and more numerous meshes. Veins meet pinnule margin at about 90° and produce vein

density of 4·5–5·0 per mm on pinnule margin. Adaxial costal epidermal cells elongate, sub-rhomboidal, up to 200 μm long and 20 μm wide; adaxial intercostal cells shorter, more irregularly polygonal, up to 120 μm long and 30 μm wide. Abaxial costal epidermal cells elongately subrhomboidal, up to 160 μm long and 30 μm wide; abaxial intercostal cells irregularly polygonal, more or less isodiametric, up to 35 μm in size. Anomocytic stomata restricted to abaxial intercostal fields; guard cells 25 μm long and 6 μm wide. Trichomes only on abaxial surface, 25–30 μm in diameter at base.

Remarks. The above emended diagnosis is based mainly on Laveine (1967), with the addition of epidermal features.

Distribution. Bolsovian and lower Westphalian D (*Paripteris linguaefolia* and *Linopteris bunbnrri* Zones *sensu* Cleal 1991) of the so-called paralic-belt of coalfields, that extends from Cape Breton (Nova Scotia) in the west, through Britain, northern France, Belgium, The Netherlands, northern Germany and Poland, to the Ukraine in the east.

Satellite form-genus BARTHELOPTERIS gen. nov.

p1941　　*Reticulopteris* Gothan, p. 427.

Type species. Barthelopteris germarii (Giebel) Zodrow and Cleal comb. nov.

Diagnosis. Pinnules entire-margined, oval to linguiform, with lateral margins parallel or slightly tapered. Pinnule apex round. Pinnule base cordiform, generally narrowly attached to rachis. Midvein usually extends for two-thirds or more of pinnule length, except in the smallest pinnules where it extends for half or less of their length. Lateral veins clearly marked, anastomosed, with dimension of the meshes diminishing towards the pinnule margin. Ultimate pinnae terminated by single apical pinnule. Frond composed of at least bipinnate segments. Isodiametric, polygonal epidermal cells more or less uniformly distributed on adaxial surface of pinnules, except near midvein where they are more elongate. Well-developed anticlinal walls on abaxial foliar cuticle. Cyclocytic stomata found only in intercostal fields of abaxial epidermis. Multicellular trichomes on both surfaces of pinnules.

Barthelopteris germarii (Giebel) Zodrow and Cleal comb. nov.

Text-fig. 5C–D

　*1857　　*Lonchopteris Germari* Giebel, p. 301, pl. 1.
　1862　　*Dictyopteris Schützei* Roemer, p. 30, pl. 12, fig. 1.
　1864　　*Sagenopteris taeniaefolia* Göppert, p. 127, pl. 9, figs 11–13.
　1897　　*Linopteris Germari* (Giebel) Potonié, p. 154.
　1941　　*Reticulopteris germari* (Giebel) Gothan, p. 428.
　k1962　　*Linopteris germari* (Giebel) Potonié; Barthel, p. 31, pl. 27, figs 1, 4, 6; pl. 28, figs 1–6.
　†1964　　*Reticulopteris germari* (Giebel) Gothan; Wagner, p. 26, pl. 17, figs 35–37.
　†1968　　*Linopteris germari* (Giebel) Potonié; Vetter, p. 105, pl. 27, fig. 5; pl. 33, fig. 3; pl. 35, figs 6–7.
　k1976　　*Reticulopteris germari* (Giebel) Gothan; Barthel, p. 94, pl. 32, figs 7–8.

Type specimen. Holotype figured with protologue originated from the Löbejün Mines in the Saale Trough, near Halle, southern Germany. Stratigraphical details were not given, but the specimen probably came from the Stephanian C Wettiner Schichten (*Sphenophyllum angustifolium* Zone *sensu* Cleal 1991). Its present location is unknown.

Emended diagnosis. Mainly elongate, linguiform to subfalcate pinnules 20–60 mm long, 3–13 mm wide, attached alternately or sub-oppositely to the rachis by a short pedicle; lateral margins parallel or slightly converging, apex obtuse, and base cordate. Prominent midvein extending for most of pinnule length. Anastomosed lateral veins form on average four small meshes between the midvein

and the pinnule margin. Lateral veins narrowly attached to midvein, and meet pinnule margin at about right-angles. Adaxial foliar epidermal cells mostly isodiametric and polygonal, 30–50 μm in size, except near midvein where they are more elongate, 50–80 μm long by 15–20 μm wide. On abaxial foliar surface, costal cells elongate, 30–60 μm long by 15–20 μm wide; intercostal cells small and irregular in shape, 14–20 μm in size. Stomata dense, irregularly orientated, probably sunken; guard cells 12–15 μm long by 7–9 μm wide; each stoma surrounded by 6–10 small subsidiary cells. Hair bases thickly cutinized, 50–80 μm in diameter.

Remarks. The above diagnosis has been adapted mainly from Vetter (1968), with some additional gross-morphological characters mentioned by Wagner (1964), and details of the epidermal structures given by Barthel (1962).

Distribution. Upper Barruelian to Autunian of the intra-montane basis of southern Portugal, southern and central France, southern Germany, Italy and Yugoslavia. In northern Spain, it ranges down to the upper Cantabrian. This stratigraphical discrepancy of the Spanish records may be because they represent drifted remains from extra-basinal ('hillside') vegetation, not normally preserved in the other areas (Knight 1974).

DISCUSSION

The evidence presented here is further confirmation that *Reticulopteris* Gothan is closely related to *Neuropteris* Sternberg *emend.* Cleal *et al.* (1990), differing significantly only in having anastomosed veins. We further provide evidence that *Neurocallipteris* Sterzel *emend.* Cleal *et al.* (1990) also had an anastomosed veined counterpart, which we have named *Barthelopteris*. These are not unique among the trigonocarpalean fronds (Wagner 1958), other well-documented form-genus couplets with anastomosed and open venation being *Lonchopteris/Alethopteris* and *Linopteris/Paripteris*. Some of the other examples quoted by Wagner are less well established. For instance, he proposed the form-genus *Anastomopteris* as a counterpart to *Odontopteris*, but it was described from a single small specimen of uncertain affinities from Turkey (Laveine 1967). The evidence put forward by Asama (1981) also undermines the link between the Cathaysian *Emplectopteridium* and the mainly Euramerian *Callipteridium*, since the former seems not to have possessed a bipartite frond architecture. Nevertheless, the general thesis that many of the open-veined trigonocarpalean fronds had anastomosed-veined counterparts still holds good.

At least among gymnosperms, such form-genus couplets appear to be unique to the trigonocarpaleans, perhaps reflecting that they are the oldest known plants to develop this style of venation. The only extant order with both types of venation is the Gnetales (as currently defined by e.g. Martens (1971)) with *Gnetum* being anastomosed and *Welwitschia* open veined. However, they cannot be regarded as couplets in the same sense as the trigonocarpalean form-genera; *Gnetum* has oval leaves with a midvein and anastomosed lateral veins, not unlike some dicot angiosperms, while *Welwitschia* has elongate, strap-like leaves with parallel veins. Indeed there is now some suggestion from rRNA data that the two genera are only distantly related and that the Gnetales is not a natural order (Troitsky *et al.* 1991). In the fossil record, the nearest comparison is with the Arberiales ('glossopterids'), where there are leaves with anastomosed (e.g. *Glossopteris*) and open (*Rhabdotaenia*) veining. Even here the anastomosed and open-veined leaves are not otherwise virtually identical as in the Trigonocarpales.

Apart from the gymnosperms, the existence of open and anastomosed veining in closely related genera is known only in ferns. Bower (1923) mentioned examples among the Ophioglossaceae, Marattiaceae, Schizaeaceae and Dennstaedtiaceae. However, anastomosed veining seems to have evolved rather later (probably in the early Mesozoic) and in quite a different way than in the gymnosperms. According to Bower, it first developed by the fusion of the distal vein-endings to form loops, and only later developed in more proximal positions in the pinnule. This contrasts with the lateral fusion of flexuous veins, which Josten (1962) showed in the gymnosperms.

The change from open to anastomosed venation occurred independently in several phylogenetic

lineages within the Trigonocarpales, but in only one has the actual transition been observed directly in the fossil record, i.e. from *Neuropteris* to *Reticulopteris* (Josten 1962; Laveine 1967). This is of general interest, as being one of the very few examples of phyletic gradualism to be documented in the plant fossil record. However, it is also of major importance for understanding the evolutionary processes taking place within the trigonocarpaleans. The gradual increase in flexuousness of the veins, which culminated in the anastomosed condition, seems to have started in the early to mid Duckmantian, and full anastomosis appeared in the early Bolsovian. It thus coincides with changes occurring in the flood-plain swamps documented by DiMichele *et al.* (1985), in which lycophyte trees favouring the wettest conditions (e.g. *Lepidophloios*, *Diaphorodendron*) were progressively replaced by trees favouring somewhat drier substrates (e.g. *Paralycopodites*). DiMichele *et al.* (1985) interpret this in terms of climatic change, referring to the Duckmantian/Bolsovian as their First Dry Interval. It is thus clearly tempting to relate the change from open anastomosed veining as a response to this climatic change.

According to the DiMichele *et al.* (1985) model, the Westphalian D experienced a reversion to wet conditions when the diaphorodendrids and lepidophloiids return to the main parts of the swamps. This is again mirrored by developments among the trigonocarpaleans, with the introduction of a second group of neuropterids, often referred to as the *N. ovata* Group. *Reticulopteris* persisted through part of the Westphalian D, but this may reflect ecological partitioning within the raised habitats (levées, etc.) favoured by the trigonocarpaleans. The areas that were topographically higher, or had drier substrates, perhaps favoured *Reticulopteris*, the lower or wetter parts, *Neuropteris*. By the middle Westphalian *Reticulopteris* disappears from the fossil record. This may reflect the elimination of the slightly drier sub-habitats of the levées, as wetter conditions became more prevalent. Alternatively, *Reticulopteris* may have been displaced by another group of trigonocarpalean plants, which bore fronds known as *Odontopteris* Brongniart, and which may have been better-adapted to the drier parts of the levées.

The evidence thus suggests that the development of anastomosed veining was a response to the climate becoming drier. However, this veining pattern did not appear suddenly, and the adaptive significance of the change must be sought in the morphological changes that preceded it, i.e. the increasing flexuousness of the veins. If this group of plants was being placed under increased physiological stress due to reduced water-availability, any improvement in the plant's water transport system for example by increasing the area of interface between the veins and the mesophyll would be an advantage. This could be achieved by either increasing the number of veins in the leaf, or increasing the length of an individual vein in a particular area of leaf. The *N. obliqua* group of species appears to have followed the latter route, by making the veins sinuous along their length. The degree of sinuosity progressively increased, in turn increasing the vein–mesophyll contact area and thus the efficiency of water distribution, until eventually adjacent veins met to form the anastomosed pattern seen in *Reticulopteris*.

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